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BIOLOGY AND IMMATURE STAGES OF SNAIL-KILLING FLIES BELONGING TO THE GENUS *TETANOCERA* (INSECTA: DIPTERA: SCIOMYZIDAE). II. LIFE HISTORIES OF PREDATORS OF SNAILS OF THE FAMILY SUCCINEIDAE

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Abstract

Information on the life histories and larval feeding habits of four Nearctic species of *Tetanocera* that prey on snails belonging to the pulmonate snail family Succineidae are presented. The four species are quite prey-specific, as larvae of *Tetanocera melanostigma* Steyskal prey on species of *Succinea,* those of *T. oxia* Steyskal and *T. spirifera* Melander attack snails of the genus *Catinella,* and larvae of *T. rotundicornis* Loew are associated with the genus *Oxyloma.* All four species are multivoltine and occur in marshy or swampy habitats containing large populations of succineid snails.

Introduction

This is the second of a series of papers covering the life histories and larval feeding habits of the North American species of *Tetanocera.* The first paper (Foote, 1996) reviewed literature, gave information on rearing techniques, and discussed the biology of two species whose larvae attack shoreline-inhabiting pulmonate snails.

In this paper I present information on the life histories of four species of *Tetanocera, T. melanostigma* Steyskal, *T. oxia* Steyskal, *T. rotundicornis* Loew, and *T. spirifera* Melander, whose larvae prey on species of succineid snails. The larval feeding habits are described, and information on trophic and spatial resource partitioning in this guild of snail-killing *Tetanocera* is presented.

Species of the three North American genera of pulmonate snails belonging to the family Succineidae are commonly called "amphibious" because of their occurrence in wetland habitats, even though they are not able to survive prolonged submersion. They are frequently encountered in shoreline habitats, although *Succinea ovalis* Say is more common in swampy and mesic forests. Species of *Oxyloma* seemingly prefer open herbaceous marshes, whereas *Catinella* species more commonly occur in shaded habitats beneath shrubs and along the wooded banks of streams.

Life Histories

Tetanocera melanostigma Steyskal

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts, and Letters, 44:60.

Tetanocera melanostigma is restricted to the Nearctic region (Knutson et al., 1986), where it is known to range from New Hampshire to Ontario and south to New York and Ohio (Fig. 1).

This species was taken in central New York and northeastern Ohio in moist to

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Fig. 1.—Distribution of *T. melanostigma.*

wet floodplain forests and around shaded hillside seepages at the foot of forested slopes. Two sites were especially productive of flies. The first site was the floodplain bordering the outlet stream of Cayuta Lake in Schuyler County, New York, where a swamp forest is broken into a mosaic of habitats. The forest canopy, composed mostly of American elm (*Ulmus americana* L.), is irregularly broken and allows considerable illumination to reach the forest floor. As a result there is a luxuriant, if discontinuous, herbaceous layer. Colonies of cattail (*Typha latifolia* L.) are found in the wetter, more open sites, and there is a thick layer of decaying leaf litter in the more forested areas. The soil is permanently moist, and during the spring months the whole area commonly is covered by 3 cm or more of water. When the area was visited during early September, *Succinea* snails, the preferred food of the larvae, were most abundant on the leaves of cattail, although adults of *T. melanostigma* were more widely distributed over the floodplain. Unfortunately, no larvae were found in the snails collected at this site. The second locality visited was a seepage located at the foot of a forested, northwest-facing slope lying along the Ringwood Branch of Cascadilla Creek about 11 km east of Ithaca, New York. The area is well shaded by deciduous trees and covered by a luxuriant layer of herbs, mostly pale touch-me-not (*Impatiens pallida* Nuttall) and joe-pye-weed (*Eupatorium maculatum* L.). The highly organic soil is always wet and may be submerged during the spring and early summer months. *Succinea* snails were abundant on the leaves of the joe-pye-weed, less common in the stands of *Impatiens,* and quite rare on a narrow-leaved species of *Carex.* All snails were inactive and attached to the leaves by a mucous secretion when collected on July 14 and 30. Four (11%) of the 35 *Succinea* collected on July 14 contained one or more larvae of *T. melanostigma,* but a larva was found in only one (4%) of 23 snails taken on July 30.

Throughout the summer, many viable eggs were obtained from both feral and laboratory-reared females. Most eggs were placed on peat moss in the jars, but a few were scattered over the glass walls. Although eggs were not found in nature, it is probable that they are deposited on vegetation near the snail prey. The incubation period lasted five to seven days under laboratory conditions (n = 35).

Observations were made on the activities of 20 first instars that hatched during the summer months. Groups of five to eight larvae were placed in each of several large Stender dishes containing moist sand and one or two living *S. ovalis.* The larvae moved slowly over the sand, stopping frequently and lifting the anterior parts of their bodies off the substrate and waving them to and fro. When they brushed against a *Succinea,* larvae became highly excited and attempted to crawl up onto the shell. Many then crawled onto the lateral surfaces of the expanded foot and attempted to insert themselves between the foot and the collar forming the edge of the mantle. However, only 14 (70%) of the 20 larvae actually managed to invade seven snails. Other larvae either failed to contact their potential prey or became entangled in the mucous secretion produced by the snails. These latter larvae invariably succumbed and were later found imbedded in small pellets of mucus along the sides and bottoms of the rearing dishes. Examination of three infested snails three or four days after larval attack revealed that each had one to three larvae embedded between the foot and mantle collar. One had three larvae along one side of the foot, and the other two each had a larva present on one side of the foot. No larvae had invaded the breathing orifice of the snails, although three were lying on either side of the opening. The snail containing three larvae remained alive for five days, apparently succumbing when the larvae molted to the second instar. This snail decayed rapidly after its death, but the larvae continued to feed for another day on the decomposing flesh. The following day, all three larvae had left the shell and were crawling about on the moist sand. A living, uninfested *Succinea* was added to the dish, and by the next day, two of the larvae were embedded between the foot and the mantle collar. The third larva had died. The two living larvae continued to feed on the snail and molted to the third instar, but only one larva managed to complete development and form a puparium. The second larva was found dead on the moist sand. In all, only two puparia were obtained from the 14 larvae that initially had infested the *Succinea* snails. Both puparia were formed in the moist sand.

The four *Succinea* containing five larvae collected on July 14 were placed in individual Stender dishes containing moist, coarse sand. One snail was alive, but very feeble, and retracted into its shell when collected from a sedge leaf. Its breathing orifice opened and closed spasmodically, and waves of faint tremors passed over its foot. Two second-instar larvae were imbedded between its foot and mantle collar. Each larva had most of its body buried in the snail, and only the posterior spiracles were visible at the surface of the prey. On the morning of July 16, the snail was dead, but both larvae were still in place laterad of the foot. Two second-instar cephalopharyngeal skeletons and one posterior spiracular disc were recovered from the decaying foot of the snail, indicating that both sciomyzid larvae had molted to the third instar. By July 17 the snail had been reduced to a few shreds of tissue, and only one larva was still within the shell. The second larva was lying quietly on the sand. Another *Succinea* was placed in the Stender dish, and by the following day it was invaded by the larva that last left the original snail. A third *Succinea* was added to the dish on July 18. On July 19 both larvae had vacated the snails and lay on the moist sand. The *Succinea* added the previous day was alive, although inactive, and unattacked. On July 20, one larva burrowed into the sand, while the other invaded the *Succinea.* The snail soon showed distress by producing frothy bubbles around its breathing orifice and a dark yellow mucous secretion on its foot. The snail was quickly killed and largely consumed, and by July 21 both larvae had formed puparia below the surface of the sand.

Another snail was not observed to contain a larva until July 17 when its retracted condition, waves of faint tremors passing over its foot, and an abundance of frothy bubbles around the breathing orifice indicated that it was in distress. At first, no larva could be seen, but within a minute, a small second instar thrust its posterior spiracles to the surface of the flesh laterad of the foot. The snail finally died on July 23, nine days after being collected, presumably harboring a developing larva all that time. By the ninth day the larva had moved to a position outside the mantle against the parietal wall of the shell. By the following day the snail was badly decomposed and partly covered by fungal hyphae, but the larva, now a third instar, was still within the host's shell, although not in a feeding position, as its head was directed away from the decaying flesh. On July 26 the larva left the snail and partly buried itself in the moist sand, where it underwent pupariation during the night of July 27.

None of the five larvae found in the four field-collected *Succinea* attacked a second snail, except for the two in the first described snail whose food supply had been restricted by intraspecific competition. All larvae killed their prey and all partly or completely buried themselves in the moist sand before undergoing pupariation. The various rearings indicated that larvae of *T. melanostigma* tend toward parasitoidism, as they remain within the food snail for extended periods of time before killing it and probably are capable of completing development within one large snail not containing other larvae. However, they may leave decaying and largely consumed snails to attack another living prey.

Under laboratory conditions the first larval stadium lasted six to eight days; the second, three to five days; and the third, from five to 11 days ($n = 10$).

Usually a few hours intervened between the time a larva left its snail food and pupariated. Some larvae pupariated within four hours after leaving their hosts, but others waited nearly three days before forming puparia. All puparia were oriented parallel to the bottom of the dish or at a slight angle from the horizontal. Under laboratory conditions the pupal stage lasted 14 to 17 days ($n = 8$).

The period between emergence of a female and her first oviposition lasted from two to five days. Two females that emerged on August 11 began laying eggs on August 13, although neither fly had mated. All their eggs failed to hatch. A wild-caught female produced a total of 213 eggs over a period of 46 days (May 31 to July 15). Her daily egg production was quite variable, ranging from three to 22.

Evidently, *T. melanostigma* larvae can also develop on other species of succineid snails. Of 100 living *Oxyloma effusa* (Pfeiffer) collected at the Inlet Valley marsh on August 13, 1956, two contained a single third instar of *T. melanostigma*. The larvae pupariated in moist sand on August 30 and 31, and adults emerged on September 13 and 14.

In central New York, the earliest seasonal record for adults was May 25, 1957; the latest date was September 5, 1956. Adults were taken in each of the summer months. In northeastern Ohio, adults were collected between early June and late August. Because the life cycle requires about 45 days and females taken at various times during the summer laid viable eggs, *T. melanostigma* probably has at least two annual generations. Winter is probably passed as a pupa, although no overwintering puparia were found.

Tetanocera oxia Steyskal, 1959

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts and Letters, 44:80.

Tetanocera oxia is known only from the Nearctic region (Knutson et al., 1986), where it ranges from Alberta to Newfoundland and south to Colorado and New York (Fig. 2).

Adults were collected near Kent in northeastern Ohio, in hydrophilic vegetation in an alder (*Alnus* sp.) grove separating an open marsh and an adjacent lowland forest. *Tetanocera rotundicornis* was more common in the more open areas of the marsh. At Butternut, Minnesota, *T. oxia* was found in a completely unshaded, grass–sedge meadow (L. V. Knutson, personal communication). In Montana, adults were collected from a mixture of herbaceous and woody vegetation, mostly shrubby willows (*Salix* spp.), bordering an open marsh. Other species of Sciomyzidae commonly collected with *T. oxia* included *Atrichomelina pubera* (Loew), *Pherbellia griseola* (Falle'n), *P. nana* (Falle'n), *P. vitalis* (Cresson), *Antichaeta borealis* Foote, *Renocera brevis* (Cresson), *Tetanocera annae* Steyskal, *T. fuscinervis* (Zetterstedt), *T. plebeja* Loew, and *T. rotundicornis*. Gastropods that were particularly abundant in habitats supporting good populations of *T. oxia* were species of *Catinella* and *Oxyloma* and slugs of the genus *Deroceras*. Aquatic snails were also common and became stranded as water levels dropped during the summer months.

Rearings were initiated from two females and three males collected June 1–4 around the margins of a sedge marsh near Kent, Ohio.

Adults collected on June 1 mated on June 2, and a female began ovipositing on June 15. Only one male and one female survived more than 30 days in the

Fig. 2.—Distribution of *T. oxia.*

laboratory. The male lived until September 5, and the female lived until September 15. This female deposited 99 eggs between June 15 and September 2. Most eggs were scattered over the peat moss substrate in the breeding jar, but 22 were attached to the cheesecloth covers and eight were affixed to the glass walls. Seven eggs were placed along the edges of a blade of grass. In nature, eggs probably are scattered on low-growing herbaceous vegetation or possibly scattered on the moist surface litter. The incubation period lasted five to seven days, and nearly all eggs were viable.

Because *T. oxia* is closely related to *T. rotundicornis,* a predator of *Oxyloma,* and because snails of the family Succineidae were abundant in the adult habitat, the newly hatched larvae were exposed to individuals of the three genera of this snail family as well as to species of more aquatic and terrestrial snails. The larvae of *T. oxia* ignored species of *Gyraulus, Aplexa, Physa, Helisoma, Planorbula, Lymnaea,* and polygryid land snails, but did respond positively to the three succineid genera.

Newly hatched larvae were quite active and constantly wandered about the rearing dish. They showed a distinct tendency to crawl up the sides of the dish, and many desiccated on the lid. Although they crawled over all species of gastropods introduced to the dish, they were particularly attracted to *C. avara* (Say). In contrast, they displayed little or no interest in the other two succineid genera, *Oxyloma* and *Succinea.* Larvae first moved up onto the shell of *Catinella* and wandered about for a few minutes until they made contact with the fleshy mantle exposed in the aperture of the shell. Larvae then moved onto the mantle and attempted to implant themselves between the collar of the mantle and the side of the foot like newly-hatched larvae of *T. rotundicornis.* Up to four larvae were found in any one snail, but usually only one or two larvae were found in place. Most larvae came to rest near the breathing pore of the snail but several embedded themselves at the anterior end of the foot. Larvae remained in place for at least three days while they molted into the second instar, although only 12 managed to reach this stage. Only three molted into the third instar. One of these eventually formed a puparium. Many larvae apparently were rubbed off the surface of the snail's flesh as it moved across the substrate. Other larvae became trapped in accumulations of mucus. Infested snails remained alive for four to ten days and most remained active. However, a few snails affixed themselves to the wall or lid of the rearing dish and remained inactive while being consumed by the fly larvae. Snails infested by two or more larvae generally died two to four days earlier than individuals with only one larva. Most snails died shortly after the larvae molted into the third instar. Larvae generally remained between the foot and mantle collar until they approached the final instar. Late in the second stadium or early in the third, larvae typically moved to a position between the mantle and shell. Larvae abandoned their snails and became free-roaming predators shortly after the prey expired. The single larva that eventually formed a puparium remained within its original snail host until shortly after its second molt, but it killed an additional five snails in the third stadium. Although newly hatched larvae refused to attack *Oxyloma* and *Succinea,* the third instars were more catholic in their diet and attacked snails belonging to all three genera of Succineidae. When an older larva contacted a snail, it quickly moved up onto the mantle and implanted itself between the mantle and the shell. The snail was killed within a few hours, and the larva rarely remained with the snail for more than ten hours. During the one- to three-day intervals between feedings, larvae remained inactive in the peat moss.

The first stadium lasted two to four days ($n = 4$); the second, two to six days ($n = 4$); and the third, about 17 days ($n = 1$). The larva that matured did not feed for four days prior to pupariating and remained buried in the peat moss. The pupal period was 20 days.

With an incubation period of five to seven days, a larval period of 21 to 27 days, and a pupal period of 20 days, the total developmental period was 46 to 54 days. No evidence of a diapause stage was obtained. At least two generations a year are produced at the latitude of northeastern Ohio. The discovery of two floating puparia in a marsh near Ithaca, New York, on April 22 suggested that overwintering occurs as a pupa. Adults emerged from these overwintering puparia on April 29, seven days after the puparia were placed under room temperatures. The earliest (May 6) and latest (August 13) collection dates for adults were both obtained near Butternut, Minnesota. In central New York, the earliest seasonal record for adults was June 10; the latest date was September 4. In northeastern Ohio, adults were collected between mid-May and mid-July, but were most common in mid-June. As a result of severe droughts in Ohio during the summers of 1987 and 1991, succineid populations were greatly reduced. As would be expected, populations of succineid predators have suffered, and no adults of *T. oxia* have been collected by me despite repeated effort in northeastern Ohio since 1992.

The larva is very light gray, similar to that of *T. rotundicornis.* The body wall appears velvety when dry, far more transparent when wet, with heart, intestine, tracheae, and Malpighian tubules very evident. Larvae of *T. oxia* lack the conspicuous body tubercles and float hairs that characterize aquatic larvae in this genus, and the lobes of the posterior spiracular dics are reduced.

Available evidence indicates that the larval feeding habits of *T. oxia* are very similar to those of *T. rotundicornis, T. melanostigma,* and *T. spirifera.* As with the larvae of these other species, those of *T. oxia* feed as parasitoids on Succineidae, living within the snails for prolonged periods before killing them. Like all other tetanocerine parasitoids (Berg, 1961; Berg and Knutson, 1978), these larvae evidently leave the host snail shells to pupariate in or on the soil or in ground litter.

Tetanocera rotundicornis Loew

1861. Berlin Entomologische Zeitschrift, 5:344.

Restricted to the Nearctic region (Knutson et al., 1986), *T. rotundicornis* is recorded from Ontario west to Alaska, south to North Carolina, Tennessee, and Oregon (Fig. 3).

In northeastern Ohio, central New York, and Idaho, adults were found most commonly in open vernal and permanent marshes containing large populations of *Oxyloma* snails. However, they do not occur in all habitats containing large *Oxyloma* populations. They tended to be more common in unshaded sites. Adults were not taken in wooded swamps, around shaded hillside seepages, or along sluggish woodland streams, although *Oxyloma* snails frequently were abundant in such habitats.

Rearings were initiated from larvae, puparia, and adults taken at the Inlet Valley, Floral Avenue, and White Church marshes in Tompkins County, New York, and from a large marsh located 9.6 km east of Kent, Portage County, Ohio.

Eggs were deposited repeatedly by laboratory-reared females and by wild-type adults collected in June, July, and August. Over two-thirds of the eggs were placed on projecting sprigs of peat moss used as a substrate in the breeding jars, but several were placed on short lengths of *Typha* and on the glass walls. Less than ten were laid on the shells of living *Oxyloma* and other snails. Eggs were mostly scattered over the substrate, and no clusters of more than four eggs were observed.

Fig. 3.—Distribution of *T. rotundicornis.*

Under laboratory conditions, hatching occurred in seven to ten days (n = 28, Inlet Valley marsh).

The newly hatched larvae were quite active and moved rapidly, if erratically, over the substrate. They stopped frequently and waved the anterior fifth of the body back and forth in the air. Once contact was made with the flesh of an *Oxyloma* snail, the larva attempted to move up onto the expanded foot, where it crawled about slowly. After these exploratory movements, larvae usually attempted to insert themselves between the foot and the collar of the mantle, but a few came to rest outside of the mantle against the shell. Many larvae became trapped and died in the mucus of the snail, and others were rubbed off the foot as snails glided over the rough substrate. As many as five larvae were found embedded up to their posterior spiracular discs in one snail, but usually only one or two larvae were found in each snail. Larvae infested only succineid snails belonging to the genus *Oxyloma,* and attempts to rear them on snails of other families were unsuccessful. In central New York and northeastern Ohio, the snail species utilized as larval food is *O. effusa,* but elsewhere in North America other species are used. In Alaska, Berg (1953) found larvae attacking *O. decampi gouldi* Pilsbry.

On July 2, 20 larvae that hatched from eggs obtained on June 25 were placed in four rearing dishes, each containing two living *O. effusa.* Only one snail was infested by July 10, and it contained two second instars. The remaining 18 larvae were found dead in balls of mucus or desiccated on the sides and tops of the rearing dishes. By July 12 the moribund infested snail had secreted an epiphragm across the shell aperture and had attached itself to the wall of the dish. Its breathing orifice opened and closed sporadically and faint tremors passed over its retracted foot. One larva was located laterad of the foot, but the second larva had temporarily disappeared. On July 16 both larvae were in the third instar. One was lying on the moist sphagnum and when placed on a living snail did not attack and quickly returned to the moss, where it died the next day. The other larva had also left the original snail and had embedded itself up to its spiracular disc in a second *Oxyloma.* This snail was inactive, retracted, and attached to the wall of the dish. By July 18, the larva had left the second snail and was lying on the glass lid of the dish with its gut filled with food. Other living *Oxyloma* were added, and the larva consumed two more individuals before forming a puparium in the peat moss on July 24. It had remained a larva for 22 days (July 2 to 24).

On July 5, 11 larvae were obtained from eggs laid on June 28. The larvae behaved similarly to those of the first rearing, and the one larva that completed development consumed three snails before pupariating on July 24. No other larvae reached the third instar. Perhaps they were unable to develop in the rearing dishes as the dead snails began to decay. Other rearings initiated from eggs were unsuccessful, for although many larvae began feeding on the *Oxyloma* snails, all died while still within the decaying bodies of the snails.

Oxyloma collected in nature frequently contained larvae of *T. rotundicornis.* Collections of 100 snails made weekly at the Inlet Valley marsh between May and September produced 12 larvae. The first larva was found on June 13; the last, on September 26. Infestations remained at low levels (zero to three infested snails per week) throughout the summer. Although a few snails contained two larvae, only one larva was able to complete development on the original snail. The other larva either died or attacked a second *Oxyloma.*

My rearing records indicate that *T. rotundicornis* larvae are predaceous but show parasitoid tendencies. They developed only on succineid snails, fed on a snail for several days before killing it, and killed only a few individuals during larval life. The larvae lack float hairs, are light colored, and have greatly reduced lobes around the posterior spriacular disc, all characters found in larvae adapted to feeding on terrestrial snails.

Puparia obtained from laboratory-reared larvae always were formed away from their prey, usually on or slightly buried in the shredded peat moss. The 65 puparia collected in nature between February and May were also found apart from shells; nearly all were floating at the water surface among emergent vegetation. Because the puparia lack float hairs and do not have the posterior end upturned, they are not well adapted for floating compared to the truly aquatic species (Berg and Knutson, 1978). They probably are formed on moist soil during the late summer and are carried into open water when the marshes refill with water during the following spring. The five puparia obtained in the laboratory rearings produced adults in 12 to 15 days. Of the 65 puparia collected in nature, 38 (59%) produced adults in 12 to 18 days when brought into the heated laboratory.

Reared females were seen to copulate two days after emerging, and copulation was repeated frequently during succeeding days. Mating lasted from less than ten minutes to more than two hours. Fertilized females began ovipositing within five days after emerging. An unfertilized virgin female laid 26 eggs in 18 days. Records were not obtained of the number of eggs laid by laboratory-reared females, but two individuals field-collected on June 20 subsequently deposited 108 and 248 eggs each in 32 days (June 25 to July 27). Adults lived in the breeding jars up to 38 days.

In central New York, the earliest seasonal record for adults was obtained on May 23; the latest record was on September 4. Adults commonly were taken throughout the summer. Probably there are at least two generations per year, as the life cycle can be completed in 56 days. No cessation of development other than that due to cold weather was observed. A puparium formed on October 5 by a larva collected on September 26 at the Inlet Valley marsh produced an adult in 14 days. That overwintering takes place in the pupal stage is indicated by the discovery of puparia containing viable pupae as early as February 9 at the Inlet Valley marsh in New York. Puparia were collected commonly during March, April, and early May.

Seventeen puparia collected in the field during March and April produced ichneumonid wasps. Six (29%) of 21 puparia collected between March 27 and April 2 at the Floral Avenue marsh gave rise to ichneumonids, and records acquired over several years indicate that the rate of parasitization varies from three to 40%. Apparently at least two species of Ichneumonidae are involved.

Tetanocera spirifera Melander

1920. Annals of the Entomological Society of America, 13:330.

Tetanocera spirifera is restricted to the Nearctic region, (Knutson et al., 1986), where it ranges from Manitoba west to Alaska, and south to Colorado and Idaho (Fig. 4).

Adults were taken in open freshwater marshes in which water levels fluctuated greatly, although specimens were not taken in marshy habitats which became dry in summer. In southwestern Montana, adults were taken by sweeping sedges and grasses along a small, mostly unshaded stream. In Colorado, Alberta, and Alaska, adults were taken in open marshes dominated by sedges (*Carex* spp.). Succineid snails were abundant in all habitats examined.

Rearings were initiated on June 28, 1968, from adults collected near East Creek Campground in Beaverhead National Forest in southwestern Montana. Mating was observed in the breeding jars on June 30, and the first eggs were deposited

Fig. 4.—Distribution of *T. spirifera.*

on July 1. Two females deposited a total of 106 eggs in 25 days either onto projecting sprigs of peat moss or affixed to the glass walls of the breeding jars. Five eggs were placed on the shells of dead *Oxyloma.* No clustering was noted, and eggs were scattered widely over the substrate.

The incubation period lasted five to six days (n = 25) under laboratory conditions. Because the newly hatched larvae lacked interspiracular processes (float hairs) and had reduced lobing around the posterior spiracular disk, it was assumed that they were more terrestrial and probably fed on shoreline or land gastropods. Small individuals of genera of fingernail clams (*Sphaerium*), aquatic snails (*Aplexa, Helisoma, Lymnaea, Physella*), succineid snails (*Oxyloma, Catinella, Succinea*), land snails (*Discus, Gyraulus, Zonitoides*), and slugs (*Deroceras*) were added to the rearing dishes. After 24 hours of exposure to these molluscs, no attacks on any of the genera of fingernail clams, aquatic or land snails, or slugs had occurred. However, larvae did display interest in the genera of Succineidae and were particularly attracted to a species of *Catinella.* After another 24 hours, first instars were found in several specimens of that genus, but no snails of the genera *Oxyloma* and *Succinea* were invaded. Most of the larvae were embedded up to their posterior spiracles in the slit that runs between the breathing pore and foot. A few larvae were embedded in the side of the foot in front of the breathing pore, and one was embedded in the anterior end of the foot. Up to three larvae were found in each snail, although most snails were invaded by only one larva. Larvae remained in place for at least two days while the snail continued to move about the rearing dishes and even feed. However, by the third day, most of the snails had retracted into their shells and several had affixed their shells to the sides of rearing dishes. Snail death usually occurred on the third day, although one snail remained alive for four days. The larvae continued to feed for another day or so after death as scavengers on the decaying snail flesh. They then abandoned the original snail host and attacked a second individual. Placement of the older larva differed from that of the newly hatched first instar in that the second instar placed itself on the flesh of the snail between the mantle and the shell. Death of the second infested snail occurred within one day, and larvae commonly then attacked a third or even a fourth individual. Older larvae were somewhat more catholic in their choice of prey in that a few individuals consumed snails belonging to the genus *Oxyloma,* however, none attacked species of nonsuccineid snails, slugs, or fingernail clams. After abandoning the final host, larvae usually buried themselves in the peat moss lining the rearing dish and remained inactive for 18 to 24 hours. The one larva that survived formed its puparium in the peat moss.

The first larval stadium lasted one to two days (n = 8); the second, two to four days (n = 4); and the third, seven days (n = 1). No adult emerged from the single puparium that was formed, so the length of the pupal period remains undetermined.

The earliest seasonal record for adults was June 10 (Pitkin, Colorado); the latest record was August 11 (Banff, Alberta). Adults have been captured during all of the summer months. No information was obtained on overwintering habits or on voltinism.

DISCUSSION

How are resources, including space, food, and time, partitioned among these four species of *Tetanocera*? Obviously, there are differences in geographic distribution of the four species. *Tetanocera melanostigma, T. oxia,* and *T. rotundocornis* share similar geographic ranges, although the last species is somewhat more broadly distributed. In contrast, *T. spirifera* is strictly western and seemingly overlaps only *T. rotundicornis* in geographic occurrence. Also, the resource dimension involving habitat is partitioned. *Tetanocera melanostigma* was found most commonly in wet to mesic woodlands, whereas the other three species were found in more open marshes.

Food is definitely partitioned among the four species. Newly hatched larvae of *T. melanostigma* attack *Succinea,* those of *T. rotundicornis* prey on *Oxyloma,* and larvae of *T. oxia* and *T. spirifera* apparently are restricted to *Catinella.* Interestingly, the last two species that utilize a common prey occurring in open marshes have somewhat different geographic distributions (Fig. 2, 4), thus they rarely occur together. All four species seemingly have very similar phenologies and thus do not avoid competing temporally.

The biology of the four Nearctic species is very similar to that reported for *T. arrogans* Meigen in Europe. Knutson (1963) reported that the newly hatched larvae of that species are largely restricted to *Oxyloma* and *Succinea* snails, although older larvae successfully fed on two other genera of land snails.

An unexplored question deals with the possible competition for succineid snails that may occur, as at least 12 sciomyzid species (*Sciomyza aristalis* [Coquillett], *S. dryomyzina* Zetterstedt, *S. simplex* Falle'n, *Pherbellia punctata maculata* [Cresson], *Pteromicra anopla* Steyskal, *Antichaeta borealis* Foote, *A. testacea* Melander, *Hoplodictya spinicornis* [Loew], and the four species of *Tetanocera*) and two species of Calliphoridae (*Melanomyia obscura* (Townsend) and *M. ordinaria* [West]) are known to prey on snails of that family.

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Literature Cited

Berg, C. O. 1953. Sciomyzid larva (Diptera) that feed on snails. Parasitology, 39:630–636.

———. 1961. Biology of snail-killing Sciomyzidae (Diptera) of North America and Europe. Verhandlung der XI International Kongress de Entomologie, 1:197–202.

Berg, C. O., and L. V. Knutson. 1978. Biology and systematics of the Sciomyzidae. Annual Review of Entomology, 23:239–258.

Foote, B. A. 1996. Biology and immature stages of snail-killing flies belonging to the genus *Tetanocera* (Insecta: Diptera: Sciomyzidae). I. Introduction and life histories of predators of shoreline snails. Annals of Carnegie Museum, 65:1–12.

Knutson, L. V. 1963. Biology and immature stages of snail-killing flies of Europe (Diptera: Sciomyzidae). Unpublished Ph.D. dissert., Cornell University, Ithaca, New York, 390 pp. Order No. Mic 63-4822, University Microfilms, Ann Arbor, Michigan (Dissertation Abstracts, 24:445–446).

Knutson, L. V., R. E. Orth, and W. L. Murphy. 1986. Catalog of Sciomyzidae (Diptera) of America north of Mexico. Entomography, 4:1–53.